

Cannon, W. A.

A Morphological Study of the Flower
and Embryo of the Wild Oat,

Avena fatua L. 1900.

QK
495
G74C22
1900
Bot.

122
dupl

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES,
THIRD SERIES.

BOTANY.

VOL. I, No. 10.

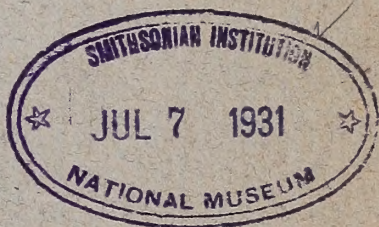
A Morphological Study of the Flower
and Embryo of the Wild Oat,
Avena fatua L.

BY

WILLIAM AUSTIN CANNON,
Assistant in Botany, Leland Stanford Junior University.

WITH FIVE PLATES.

Issued April 21, 1900.



SAN FRANCISCO:
PUBLISHED BY THE ACADEMY,
1900.

ITEE.

CHARLES H.

man.

WILLIAM E. RITTER,

G. P. RIXFORD.

EDITORS OF BOTANICAL PUBLICATIONS.

DOUGLAS H. CAMPBELL,

WILLIAM. A. SETCHELL.

Q1K
495
G74C22
1900
BOT

PROCEEDINGS
OF THE
CALIFORNIA ACADEMY OF SCIENCES,
THIRD SERIES.

BOTANY.

VOL. I, No. 10.

A Morphological Study of the Flower
and Embryo of the Cat,
Av da L.

BY

WILLIAM AUSTIN CANNON,
Assistant in Botany, Leland Stanford Junior University.

WITH FIVE PLATES.

Issued April 21, 1900.

SAN FRANCISCO:
PUBLISHED BY THE ACADEMY,
1900.



584.1
1622
copy 2

A MORPHOLOGICAL STUDY OF THE FLOWER AND EMBRYO OF THE WILD OAT, AVENA FATUA L.

BY WILLIAM AUSTIN CANNON,

Assistant in Botany, Leland Stanford Junior University.

CONTENTS.

PLATES XLIX-LIII.

	PAGE.
I. INTRODUCTION.....	329
II. ORIGIN OF THE FLORAL ORGANS.....	331
III. THE STAMEN.....	335
IV. THE EMBRYO-SAC.....	337
V. FERTILIZATION AND THE BUILDING OF THE ENDOSPERM.....	342
VI. THE EMBRYO.....	343
VII. SUMMARY.....	351
BIBLIOGRAPHY.....	354
EXPLANATION OF PLATES.....	356

I. INTRODUCTION.

THE grasses are said by Hackel to be a very isolated family, sharply defined from the other low Monocotyledons to which they are bound by only obscure relationships. For this reason they have been variously placed by systematists, but are now generally and probably best regarded as near the Aroids and the Palms. The life history of such grasses as have been studied justifies this conclusion, and it is the object of this investigation to add something to our knowledge of these forms in order that their mutual relationships may be better understood. Enough morphological work has already been done on types allied to the grasses to form a basis for comparisons. It remains therefore only for more extended and more thorough studies to be made on grasses before comparisons can be instituted. There have already been a few such studies published. The most important recent contributions to our knowledge of the life history of grasses have been by Lermer and Holzner (1888), and Koernicke (1896). The original of the former contribution was unfortunately not at hand and I was obliged

to depend on citations and fragmentary reviews for my knowledge of it. It is an exhaustive work, describing the complete development of the floral and reproductive organs of the cultivated barley as well as its embryology. Koernicke, on the other hand, studied the development of the stamen and embryo-sac of the wheat with especial reference to cytological phenomena. Two studies which were made before the introduction of the modern methods of imbedding and sectioning, viz. by Fischer (1880), and Nörner (1881), were consulted in the preparation of this paper. Fischer's study deals with the development of the embryo-sac of various grasses, while that of Nörner treats of the embryology alone. All of the contributions mentioned above refer to grasses belonging to the branch of the family known as the Poaceæ, the members of which, besides being closely related, have very similar habits and habitat. It is to be greatly desired that future studies of the Gramineæ may include representative grasses of various habits and habitat of both branches of the family. In this way an adequate knowledge of the inter-relationships of the grasses, as well as their relationships to other Monocotyledons may be obtained, and also a better idea of the origin of plant structures. In addition to the papers already named there is a great mass of work on the comparative morphology of the different parts of the mature flower and of the mature embryo. Beginning with Malpighi (*Omnia opera*, 1687), and Gärtner one hundred years later, the series extends with little interruption to the present. For a review of these works the reader is referred to the studies by Bruns (1892), and to the recent one by Kennedy (1899).

Because the flower of the wild oat is the type grass flower, (it is described and figured in any good text-book of botany), it was selected for this morphological study. The wild oat is supposed to be the ancestor of the cultivated species, or at least the nearest relative of that ancestor, and is one of our commonest grasses. It was presumably introduced into California at an early date from Southern Europe, and has now a wide range throughout the state.

II. ORIGIN OF THE FLORAL ORGANS.

The spikelet of *Avena* branches sympodially, the apex of the young spikelet developing into flowers and finally pistils. Each flower arises below the apex of the primordium of the spikelet and grows at right angles to it, so that the rachilla is sharply angular when young (fig. 1).

The primordium of the spikelet consists of three well defined series of tissues: (1) a dermatogen, (2) a single layer of large hypodermal cells—the periblem—which surrounds (3) an axial strand—the plerome cylinder. As the primordium increases in length the cells of the epidermis and of the periblem divide by anticlinal walls and form a continuous cap to the plerome. The plerome arises from a single cell, or perhaps a group of cells, that terminates the axial strand (fig. 3). All of these cells are well filled with protoplasm, are without conspicuous vacuoles, and have relatively large nuclei.

The floral organs all arise in much the same way upon the periphery of the primordium, beginning with the lower glume and ending with the carpel. Each begins as a ridge of tissue that extends part way around the primordium of the flower. The origin of each floral organ will be spoken of in the order of its appearance.

The lower glume and the young flower apex appear to arise simultaneously just below the tip of the primordium of the spikelet (fig. 4). At first these two rudiments are very similar, but the flower apex soon becomes broader, and the lower glume somewhat deeper by its growth and by the stretching out of that part of the rachilla that is immediately below it. At this time the glume is a semicircular organ, club-shaped in longitudinal section, composed of a well defined dermatogen enclosing about three layers of cells. As the lower glume increases in length it takes a direction which coincides with the direction of that part of the rachilla from which it springs, but it soon bends toward the tip of the spikelet (figs. 1 and 2). At that stage in the development of a flower when all of the floral organs are first to be distinguished, a narrow outgrowth appears near

the base and on the inner surface of the lower glume. This outgrowth is at first on a level opposite the lodiculæ, but as the glume increases in length, it is carried upward somewhat (figs. 1 and 2). It becomes longer and broader and forms the lamina of the mature lower glume, while the original rudiment persists as the awn.

The upper palet and the lodiculæ arise apparently at the same time and from the same rudiment (fig. 5). A crescent-shaped ridge of tissue extends nearly around the primordium. This ridge does not form on the anterior aspect, but from the ends the lodiculæ develop, and from the anterior face the upper palet. The upper palet grows as the adjacent organs develop. When it can first be plainly recognized it is composed of three layers of cells, and later becomes thicker by periclinal divisions of the cells at its base (figs. 5 and 6). The upper palet is the last of the protective organs of the oat-flower to develop.

The lodiculæ appear as rounded shoulders jutting out from the lateral surfaces of the primordium and mark the ends of the rudiment that gives rise to the upper palet (fig. 5). The apex of the young flower grows up and leaves the lodiculæ in a lateral position below its tip. The lodiculæ are at first triangular with the broad base resting against the surface of the primordium. They gradually acquire the oblong shape characteristic of the mature organs.

The stamens of the wild oat arise as conical outgrowths at equal distances apart around the periphery of the apex of the flower. Figure 1 shows the relation of the anterior stamen to the lower glume; and figure 7, which is taken from a longitudinal section made a little to one side of the center of the flower, shows one of the lateral stamens and its relation to one of the lodiculæ. The stamens develop early, the filament appearing before the lamina of the lower glume is well differentiated and while the carpel is still small. It increases in length by cell-division in all parts and is always relatively slender. The pollen is generally shed before the stigmas of the flower have protruded from the spreading glumes.

The carpel is the last of the floral organs to arise. It appears as a single ridge of tissue on the anterior side of the floral axis (fig. 6), and gradually encircles the apex of the young flower (fig. 6*a*). The young carpel is club-shaped in longitudinal section, and its structure is sufficiently indicated by the figures. Soon after the carpel has completely surrounded the tip of the flower axis, two protuberances appear on the sides and form the beginnings of the stigmas; later the rim of the carpel closes and shuts in the ovule.

A correct interpretation of the relations of the parts of the grass flower is of great importance, because upon it depends a right understanding of the relationships of this isolated family. These relationships are based mainly on the number and arrangement of the floral organs. The origin and development of the gynœceum and andrœceum of the grass flower, as well as the origin and development of the organs subtending these, are now fairly well understood, but the morphological significance of some of these organs is very much in doubt. It is not known, for instance, whether the lodiculæ represent a perianth or not, an important basal fact in determining the position of the grasses. There are concerning the lodiculæ two widely different views which have been held by botanists. In the first, the lodiculæ are considered to be the stipules of a leaf which has been suppressed, or the parts of a leaf of which the middle is wanting; and the posterior lodicula when present is held to be, according to this hypothesis, a leaf or palet which alternates with the lodicular palet and which therefore continues the distichous arrangement of the lower glume and upper palet. Or, in other words, according to this interpretation of the grass flower there are represented four alternating palets of which the two lowest persist, the others being rudiments. This explanation of the relation of the lodiculæ to the other organs of the grass flower is opposed to the law which is sometimes said to govern leaf arrangement among the grasses, by which the leaves of a branch are inserted on a plane at right angles to that of the

leaves of the main axis. Further, this hypothesis excludes the idea of a perianth in the grasses, and with this a very important clue to the connections between the grasses and other low Monocotyledons is overlooked. The second interpretation recognizes a perianth which is represented by the lodiculæ. The two anterior members are present in most grasses, and the trimerous perianth is completed by a posterior member in the bamboos and certain other grasses. Neither of the hypotheses set up to explain the significance of the lodiculæ is entirely satisfactory—the first explanation for the reasons given, and the second, mainly because of the position of the lodiculæ in most grasses. The relation of the lodiculæ to the upper palet in *Avena* (and in some other grasses as well) in which there is a common origin for both, makes it difficult to look upon the lodiculæ as members of a perianth, for this, if present, ought to originate and therefore be placed on a higher plane than the upper palet. This intimate connection of the lodiculæ and upper palet is met also in *Oryza*, *Zea*, and *Solenache* (Eichler). The lodiculæ vary greatly in number in the different grasses and assume various positions, as in the Paniceæ they are mainly outside the upper palet, and in the *Ehrharta*-species similar bracts are associated with the lower glume. From this it seems reasonable to conclude that not all of the lodiculæ can represent rudimentary perianths. In addition to this variation in position of the lodiculæ there are present in the rye (Eichler) and certain other grasses four anterior lodiculæ placed on two planes; the two lower are connected with the upper palet (“stipular lodiculæ”) and the two upper, originating evidently on a higher plane, are regarded as being two members of a perianth (“perianthal lodiculæ”). A comparison of the lodiculæ of *Avena* with those of the rye shows them to be homologous to the stipular lodiculæ of the rye, but in *Avena* the perianthal lodiculæ are wanting. In the bamboo a trimerous perianth of three lodiculæ is present, and in addition to this, two stipular lodiculæ also. The upper lodiculæ of the bamboo, by reason of their position and number, have been rightly

considered to make up a perianth. They are homologous to the perianthal lodiculæ of the rye and cannot, therefore, hold similar relations to the lodiculæ of *Avena*. I conclude then from a comparison of the grass flowers that the lodiculæ in *Avena* do not represent a perianth, but that the perianth is entirely wanting; they are homologous to the stipular lodiculæ of other grasses.

From this it would appear therefore that not all those organs called lodiculæ are necessarily or even probably the same morphologically. In some grasses they are survivals or rudiments of a perianth, in others they are survivals or rudiments of extra-floral leaves, and in still others, where two rows occur, the inner row is morphologically perianth, the outer extra-floral bracts, and there is no evidence (Eichler) of a double perianth.

III. THE STAMEN.

The development of the stamen of *Avena*, as far as followed, corresponds rather closely with that of the stamen of wheat, (Koernicke, 1896). The stamens originate as crown-shaped projections at equal distances apart on the periphery of the floral axis. A cross-section shows the young stamen to be oblong in form (fig. 8). By more rapid growth in the portions where the loculi are to appear, the outline becomes irregular and characteristic of the stamens of Angiosperms (fig. 9). A constriction occurs very early at the base of the stamen, which indicates the beginning of the filament (fig. 7). The subsequent growth of the stamen until the time when the pollen grains are ripe is due almost entirely to the elongation of the anthers—the filament growing only immediately before the pollen is scattered. The primary tissues—plerome, periblem, and dermatogen—are clearly marked in the young stamen. As usual in Angiosperms, the pollen is derived from the periblem. In the increase in diameter of the anther, preceding the cutting off of the archesporium, the cells of the periblem in the parts where the loculi are to appear become larger

than the intervening periblem cells and also than those of the plerome. They become separated from the epidermis by periclinal walls of more or less regular formation (fig. 10); but the hypodermal cells between the large periblem cells described divide by anticlinal walls only. This cell-formation results in the lobed condition characteristic of anthers.

A cross-section of an anther in which the loculi are visible shows one conspicuously large cell surrounded by two series of periblem cells and the epidermis. Of these three concentric cell series the middle one forms the endothecium, and with the epidermis persists until the anther is ripe. The inner series, according to Koernicke, divides by periclinal walls to form the tapetum and a middle layer, both of which are resorbed in the later stages of the development of the anther. This point, however, I did not see in the oat. The large cells which occupy the middle of each loculus and form, as longitudinal sections show, a single row, constitute the archesporium. Later these divide by radial walls and thus give rise to the pollen mother-cells. A median longitudinal section through a loculus in which the pollen mother-cells are formed (fig. 11) shows two rows of spore mother-cells, each of which reaches to the walls of the loculus.

The history of the division of the mother-cells into tetrads I did not follow. Koernicke gives a detailed account of this for the wheat, and we may suppose that the history of spore formation in the two nearly related genera is very similar.

The mature pollen spore is enclosed by two integuments, the inner of which is very delicate. The spore is densely filled with coarse granules of starch. Three bodies that stain strongly with the reagent used (Haidenhain's iron-alum-hæmatoxylin) are present in the spore.

The largest is oval and stains less strongly than the two spindle-shaped ones. These three are respectively the vegetative and the two generative nuclei. Some difficulty was encountered in distinguishing the nuclei from the cytoplasm in the generative cells, and it is probable that the

nuclei form a larger portion of the cell contents than is indicated in the figure (fig. 12). Koernicke does not mention a division of the generative nuclei in the pollen grain of wheat, and this would be an apparent exception to the statement by Strasburger (1884), that the division of the generative nuclei is a constant character of the grasses.

The generative nuclei in the pollen grain of *Avena* occupy various positions with relation to the vegetative nucleus, but are always parallel to each other. The vegetative nucleus is oblong and as large as both the other two nuclei combined. The development of the pollen grain was not followed further.

IV. THE EMBRYO-SAC.

The initial cell of the embryo-sac in the oat is of sub-epidermal origin. It is the middle one of the epidermal cells of the primordium, as is generally the case (Fischer), and it is continuous with the axial plerome. At the time when both of the integuments of the ovary are clearly distinguishable, the archesporial cell is easily made out by reason of its relatively large size. At this stage it occupies in the oat, as in the wheat (Koernicke), over one-third of the nucellus, and is eight to ten times as large as the surrounding cells. There is no apparent difference at this time between the archesporial cell and those of the nucellus in density of cell contents.

When the archesporial cell is first recognizable the ovule is atropous. Parallel with the development of the sister cells and of the embryo-sac, the cells in the rachilla side of the nucellus divide and grow more rapidly than those in the opposite side, and push the micropylar end over so that finally the micropyle occupies a position almost opposite from that of the archesporial cell. During the revolution of the ovule (macrosporangium) the ovary increases greatly in size, and, from being somewhat flattened at first, it becomes spherical and at last oblong. The size and position of the ovule is intimately connected with the development of the archesporial cell and the embryo-sac.

When the axis of the ovule forms a right angle with that of the flower the archesporial cell has elongated, keeping pace with the elongating nucellus, and its nucleus has undergone one division (fig. 14). The cell is densely filled with granular protoplasm; no vacuoles are visible.

There are in *Avena* as in *Eichhornia* (W. R. Smith, 1898) apparently three ways in which the sister cells may be formed. In the first, the nucleus of the archesporial cell divides after the elongation of the cell, the two resulting nuclei divide, and the four sister nuclei lie free in the protoplasm of the cell, no walls separating them (fig. 15). Or (second) after the nuclei have divided, walls may appear between them (fig. 17). However, owing to faulty methods of staining, I could not in every instance be sure of the presence or absence of the separating walls, but the phenomena were observed at various times during the course of the study. In the third manner of formation of sister cells, dividing walls followed each nuclear division as in the section represented in figure 16. This variation in the formation of sister cells was not described by Koernicke for *Triticum*, or by Fischer for any of the grasses studied by him. Fischer did however describe a condition in the genus *Melica* which he says is constant, and is analogous to what has been described above for *Avena*. In *Melica* the division of the nucleus of the archesporium is followed in all cases by the formation of a dividing wall. The two nuclei thus formed divide each once, but without cell-walls being formed; so that in *Melica* there are two cells with two sister nuclei in each cell. It would be of importance to know whether this condition is as constant as Fischer states, or whether there really is in *Melica* that variation in the formation of the sister cells which is apparently the case in *Avena* and in *Eichhornia*.

In whatever way the sister cells are formed four superimposed nuclei always result, and of these the lowest becomes the spore mother-cell, the others becoming resorbed. The uppermost of the sister cells is the first to disappear (fig. 17), and after it the two next lower ones in

succession, if cell-walls have been formed between them, or simultaneously if the nuclei are not separated by walls (figs. 18 and 19). The macrospore thus formed occupies the position recently occupied by the sister cells, and extends to the epidermis. No tapetum is formed. When they are present the walls separating the sister cells are not so strongly swollen as in *Triticum* (Koernicke) and in *Alopecurus* (Fischer, fig. 32). In this regard the oat agrees with the figures given by Fischer for *Sesleria*. The wall next to the epidermis in *Avena* is somewhat swollen as in *Sesleria* (l. c. fig. 10).

The macrospore nucleus divides into two nuclei which lie, one in the micropylar end and the other at a point distant about one-third the length of the embryo-sac from its chalaza end. The chalaza nucleus divides at right angles, and the upper nucleus divides parallel to the long axis of the embryo-sac (fig. 20). One large vacuole separates the two nuclear groups; and another separates the chalaza nucleus from the end of the embryo-sac. Each nucleus of each group divides again, the upper group at right angles to the plane of the first division. The embryo-sac now contains eight free nuclei (figs. 21 and 21a). During these divisions of the nuclei, the embryo-sac has increased greatly in length and diameter, and has absorbed the adjacent cells of the nucellus. Many large vacuoles have appeared in the protoplasm of the embryo-sac; prominent among them are the large ones surrounding the protoplasmic bridge that connects the two groups of nuclei, and the vacuole in the chalaza end.

In the micropylar end of the embryo-sac two (sister) nuclei form the synergidæ; and one that lies at one side of the synergids, the egg; while the sister nucleus of the egg becomes the upper polar nucleus (figs. 21 and 22). Three of the nuclei in the chalaza end of the sac give rise to the antipodal complex, and one forms the lower polar nucleus.

The egg is at first spherical, but as it increases in size it becomes oblong, and finally, when nearly ready for fertilization, balloon-shaped (figs. 24 and 25). It occupies a

lateral position as regards the synergidæ, which is the position of the egg in *Sesleria* also (Fischer). The synergidæ are flask-shaped and do not appear to contain vacuoles. The egg-apparatus increases greatly in size but shows no other change up to the time of fertilization.

The upper polar nucleus moves to meet the lower polar nucleus in the region of the antipodal nuclei (figs. 21 and 22). The two nuclei then move towards the egg and remain in close proximity to it, in the protoplasmic bridge that connects the egg-apparatus and the antipodals. The polar nuclei do not fuse until about the time of the fertilization of the egg. The exact time was not determined. The nucleoli of the polar nuclei are the largest in the embryo-sac and with the ordinary staining reagents become deeply colored. The peculiar behavior of the polar nuclei of the oat does not agree with that in the grasses examined by Fischer; but Koernicke indicates that some such action of the polar nuclei occurs in *Triticum*, as he states that the two polar nuclei move towards each other. The sides of the polar nuclei that are in contact with one another are flattened, and each cell retains its delicate cell-wall up to the time of fertilization, when they fuse to form the endosperm nucleus. The time of the fusion of the polar nuclei of the oat appears to be the same as that in the wheat. There is no rule as to which side of the polar nuclei will come in contact, so that a line separating them may be parallel to the long axis of the embryo-sac, at right angles to it, or it may be at any angle between the two. The endosperm nucleus is imbedded in a dense strand of protoplasm which connects the antipodals and the egg, and strands radiate from this to the walls of the embryo-sac. This last is especially true of the younger sacs, the protoplasmic threads disappearing in the older stages. The protoplasmic bridge persists however until the antipodals disappear.

The embryo-sacs of all the grasses that have been studied, except *Melica* (Fischer), show a multiplication of the antipodal cells. This phenomenon has also recently been

observed in the family which is probably the nearest ally of the grasses, viz. the Sparganiaceæ, and in the Araceæ.¹

The antipodal nuclei of the oat begin to divide as soon as the lower polar nucleus is separated from them. They divide repeatedly and each nucleus becomes enclosed in a globular mass of protoplasm. The increase in number is accompanied by an increase in the size of the cells and also of their nuclei. A good idea of this growth of the antipodal complex may be had by comparing figures 22, 23 and 25. The multiplication of the antipodals and their increase in size takes place at the expense of the nucellus (*cf.* figs. 23 and 25). The greatest number of antipodals is found at the time of the fertilization of the egg. This number was not exactly determined, but it was at least 36, which corresponds with that given by Koernicke for the wheat. There is uniformly in *Avena* as in *Triticum* one nucleus in each cell. Fischer describes three antipodal cells only for *Alopecurus* and *Sesleria*, but says that there are four nuclei in each. *Melica*, on the other hand, does not show multiplication of the antipodals in any way. When they begin to divide, the antipodal cells of *Avena* occupy a position near, but not in, the chalaza end of the embryo-sac, and a line drawn through the long axis of the embryo-sac would bisect them. As the embryo-sac develops, the antipodals assume a lateral position and retain it until they disappear.

The antipodal complex shows, in section, a characteristic crescent form; the nuclei are large and stain deeply with the common staining agents. No vacuoles are visible in the young antipodal cells, but they appear as the cells grow, and are increasingly marked during their dissolution.

The disorganization of the antipodals begins simultaneously with the formation of the endosperm, and usually they can no longer be seen at the time when the micropylar end of the embryo-sac is being filled with endosperm. Figure 27 shows the condition of the antipodals when the endosperm is beginning to form. A few large vacuoles in each

¹ Campbell, Bot. Gaz., March, 1899, and Proc. Cal. Acad. Sciences, 1899.

cell can be seen. Almost the last stages in the existence of the antipodals is shown in figure 28. The protoplasm of the antipodal cells is the first portion of the cells to disappear; traces of the antipodal nuclei are frequently met when they are quite disassociated from the protoplasm of the cells. The function of the great antipodal complex, in those forms in which it is present, undoubtedly varies with the time of its formation. In the oat, as in the wheat (Koernicke), the antipodals are formed prior to fertilization and disappear with the multiplication of the endosperm nuclei, being consumed by the endosperm in its development. In *Sparganium* (Campbell) the antipodals multiply enormously after fertilization, and evidently function as endosperm, and consequently serve to nourish the growing embryo.

V. FERTILIZATION AND THE BUILDING OF THE ENDOSPERM.

The pollen-tube enters the embryo-sac by pressing apart the cells of the micropyle. The two synergidæ do not usually disappear at this time, although one seems to do so. This point needs further study. One, or perhaps the two synergidæ, may sometimes be observed partly resorbed while the embryo is still in the proembryo stage, and it is likely here, as in the wheat (Koernicke), that both synergidæ are consumed as nourishment for the young embryo. The phenomena associated with the union of the sexual nuclei, as well as the further history of the pollen-tube, the vegetative nucleus, and second generative nucleus were not followed.

The endosperm nucleus begins to divide about the time when the egg is fertilized; but whether this precedes or follows the union of the nuclei was not determined. At the first division of the egg a few endosperm nuclei may be seen in the thin protoplasmic lining in different parts of the embryo-sac. These nuclei vary a great deal in size, and in shape also, from spindle form to a flattened sphere. Each endosperm nucleus generally contains several (three to eight) nucleoli. In the early stages in endosperm formation

the nuclei divide in all parts of the embryo-sac wherever they are. With their increase in number they become larger in size, cease dividing, are usually spherical, and become enclosed in rather dense masses of protoplasm, which later become separated by cell walls. The lumen of the embryo-sac begins to fill first around the embryo, where the endosperm cells that closely invest it are long, somewhat crescent-shaped, and very dense.

The nucellus and embryo-sac increase greatly in length after the fertilization of the egg, the embryo-sac absorbing more and more of the nucellus cells, until little more than a single layer separates it from the inner integument. A change also takes place in the integuments. Before fertilization and more especially during the youngest stages of the embryo-sac, the two integuments are quite similar, each being composed of two layers of uniform cells. After fertilization the outer integument is compressed and finally destroyed, and the inner one takes on heavier cell-walls and becomes the outer seed-coat.

VI. THE EMBRYO.

The oöspore, which is relatively small and enclosed by a delicate membranous wall, increases considerably in size after fertilization and before any division occurs. The cytoplasm is granular and with few vacuoles. An interesting variation in the cytoplasmic structure of the cells of very young embryos was met in several instances. The cytoplasm appeared very coarsely granular and net-like. No conspicuous vacuoles were present in such embryos; growth and cell-division as far as it had occurred were normal. No embryos beyond the proembryo stage presented this peculiar appearance of the cytoplasm.

The first division of the egg occurs near the distal end and is transverse, either at right angles to the long axis of the young embryo (proembryo), or at an angle more or less acute to it. I found one abnormal case in the first division of the egg, in which the cell-wall was a longitudinal one. Figure 29 shows an egg in course of the first division

in which the wall is to be at right angles to the long axis of the proembryo. The section was cut not exactly in the median plane, and the figure shows what appears to be a large vacuole near the point of attachment of the embryo. Examinations of the neighboring section show that this is not a vacuole, the only visible vacuole present being in the neighborhood of the dividing nucleus. When the first wall is formed, however, vacuoles occur in both cells, and as the further history of the embryo is traced, the greatest number of these are to be found at and near its base.

The second division of the embryo occurs in the basal cell, so that the cell-walls of the pro-embryo are formed in basipetal succession. Nörner separates the grass embryos into three groups based on the direction taken by the first two walls. His "Type I" may be represented by figure 31, in which the first wall is at right angles to the long axis of the embryo, and the second parallel to it. Figure 32 represents "Type II" of Nörner in which the first wall is at right angles to the long axis of the embryo, but the second wall cuts this at an acute angle. Such embryos as that shown in figure 30 fall under "Type III". In this embryo the first wall is at an acute angle with the long axis of the embryo, and the second strikes the first at a sharp angle. As the figures indicate, the three types given by Nörner for all grasses studied by him are present in *Avena fatua*. Of these types the first is perhaps the most common; when the others are met in old embryos, the cell formation is so confusing that it practically defies solution.

The third cell-wall is formed in the distal cell of the pro-embryo, bisecting it parallel to the long axis of the pro-embryo, and is the first cell division belonging to the embryo proper (fig. 30). The fourth division is a transverse wall formed in the basal proembryo cell and cuts off the suspensor. No subsequent division was observed in the suspensor cell. At this stage in the development of the embryo there are four segments and five cells. There are two distal cells in the first segment, and between them and the suspensor two superimposed cells, of which the second belonged to the proembryo, and the third was derived from

the basal proembryo cell, and is therefore not homologous to the cells above. For the sake of clearness in tracing its history in the developing embryo this last is designated as segment three.

The growth of the embryo is such as to obliterate these primary divisions, but a comparative study shows that probably the cotyledon and stem-apex are derived from the first segment, the hypocotyl and the initials which give rise to the root-cap, the cortex, and the dermatogen of the root from the second, and the coleorhiza from segment III. This is practically the conclusion of Nörner (l. c). As the boundary between the first and second segments particularly, in the advanced embryo, however, is not at all clearly defined, it was not possible for me to determine whether the stem-apex arose from the first segment, as in *Lilæa* (Campbell) and others, or from the second, as in *Alisma* (Schaffner, 1897).

In connection with the origin of the members of the embryo it is interesting to note that the position of the root and of the stem-apex in the embryo are the same with relation to the vertical as in the mature plant (which of course is the case in anatropous ovules in general). The reaction of the embryo to the influence of gravitation can here be traced to the one-celled stage. Experiments might be devised which would show not only the immediate influence of gravity on the embryo, but also which would give some grounds on which to base a plausible hypothesis to account for the anatropous condition of the ovule in this and in other plants where this condition occurs, and also its relation to the embryo.

Continuing the history of the development of the embryo, the next wall to be formed after the suspensor is cut off, the fifth wall in the embryo, is a vertical one in the second segment. Up to this time in the growth of the embryo the succession in cell formation is quite regular, but after this it varies considerably. The next wall to be formed is generally a vertical one in segment III, making a seven-celled embryo (fig. 33). This segment does not, however,

always divide before quadrants are formed in the first segment. Quadrants are formed in segment I first, but there is no regularity in the quadrant divisions of the other primary segments. In some embryos quadrants are formed with regularity in all the primary divisions of the embryo, beginning with the distal primary segment; but in others, as in the embryo from which figure 35 was drawn, segment III has divided only once, although quadrants had been formed in the second segment, and in the first, octants. Segments I and II show greater regularity in cell formation than the third segment in the early as well as in the later stages in the growth of the embryo.

Octants are formed in the distal segment by anticlinal walls which strike the quadrants at an acute angle, generally below the middle, and not as stated by Nörner, at right angles to them. Of the octants thus formed the four uppermost form part of the dermatogen and divide subsequently by anticlinal walls only. The octants are usually formed as figure 35 indicates, while segment II is yet in the quadrant stage. This is, however, not at all uniform, and periclinal walls are sometimes met in the second segment before the octants are completely formed (fig. 36).

As just stated, the first periclinal divisions occur in the second segment. These are followed by similar division walls in the end segment. Segment III, in which the divisions are very irregular, does not take part in the periclinal divisions above mentioned. The plerome is cut off as in *Lilæa* (Campbell, 1898) in the two end segments at about the same time. This was found also in the grasses by Nörner (l. c.). In some cases in *Avena* it occurs, at least, in the end segment first (fig. 38).

An examination of the cells of the young embryo shows an increase in number and size of the vacuoles in the micropylar end. This peculiarity, together with the irregularity of cell divisions, serves in a way to mark the descendants of the third segment.

The suspensor, which is formed when segment III is cut off, remains small, does not divide, and plays an inconspicuous part in the history of the embryo. A large vacuole

appears early in that part of the suspensor which touches the micropylar end of the embryo-sac. The protoplasm in the distal end of this cell (i. e. of the suspensor cell) rounds itself off, a membrane separates it from the large vacuole, and thus the embryo is attached to the micropyle by the proximal ends of the side walls of the old basal cell. The dotted lines in figures 33 and 34 indicate this attachment. The embryo remains connected with the micropyle in this manner until about the time when the primary tissues are differentiated, and then the attachment is broken and it lies free in the embryo-sac. The suspensor cell persists to form the end of the coleorhiza. It was not seen to divide, but it is not unlikely that in old embryos it may undergo a few irregular divisions.

The behavior of the suspensor resembles that of *Sparganium* (Campbell, 1899), but not of *Lilæa* (Campbell, 1898) and *Alisma* (Schaffner, 1896), in which the suspensor becomes a large and important absorbent organ. The degeneration of the suspensor of *Avena* is doubtless associated with the development of the endosperm cells, which closely invest the embryo, as well as with the prominent synergidæ which here, as in the wheat (Koernicke), serve to nourish the embryo in its youngest stages.

After the primary tissues are cut off, the embryo increases in size, mainly in length, by growth which is almost wholly confined to segments I and III. The embryo is club-shaped, pointed at the micropylar and blunt at the distal end. The periblem and plerome cells undergo few longitudinal divisions, dividing mostly by transverse walls. This makes the boundaries of the primitive segments difficult to trace. Cross-sections through the middle of the embryo show a plerome of about eight cells surrounded by a periblem two or three cells thick. The two are very similar, being composed of relatively large cells. The dermatogen is made up of regular and comparatively small cells. A cross-section near the micropylar end, through segment III, shows a greater irregularity in the structure of the dermatogen and internal tissues, which are not differentiated into plerome and periblem.

After the primary tissues are differentiated there are three very well-marked periods of growth, in which different sections of the embryo take part. The first is that succeeding the differentiation of the primary tissues and extends to the appearance of the stem-apex as a rounded elevation of the epidermis on the posterior surface of the embryo, and includes mainly the descendants of segments I and III. The second period is the elongation of that portion of the embryo which is above the stem-apex, the cotyledon, which takes place soon after the appearance of the plumule and plumule-sheath. The third occurs in the region of the radicle, in the descendants of the second segment of the proembryo, and takes place after the cotyledon has elongated. After these periods of growth and before the maturation of the embryo, plumule, cotyledon (scutellum), and root develop and grow simultaneously, retaining the same proportions. These periods of growth correspond very well with the further differentiation of the tissues of the embryo.

When the stem-apex is first discernible (fig. 41), the embryo is already relatively large, and all traces of its primitive segments are quite obliterated. The embryo at this period is oval with an obtuse cotyledonary and a sharp tapering radicle end. In cross-section, the embryo has changed from circular to oval. The stem-apex appears on the posterior side of the embryo about one-third the distance from the cotyledonary end, and becomes surrounded by a low ridge of tissue. From this, on the side of the stem-apex opposite, springs the epiblast, and on the cotyledonary side merely an augmentation of the boundary which separates cotyledon and plumule (fig. 41). An examination of the tissues at this stage of the development of the embryo shows several rows of elongated plerome cells in the cotyledon enclosed by a periblem of large and rather irregular cells. The epidermis of the cotyledon is beginning to assume the palisade-like structure it later develops as an absorbing organ. The elongation of the plerome cells is continued to the region of the stem-apex, but is not found in the root. This differentiation of the plerome is connected

with the sudden shooting up of the cotyledon, and doubtless these elongated cells function as food carriers from the cotyledon to the developing plumule. The differentiation of corresponding tissues in the root occurs at a much later period, but the primary root tissues are already well defined. The group of cells at the end of the plerome cylinder, which give rise to the root-cap and to the dermatogen and cortex of the root, can be easily distinguished. The plerome initials are not developed until later; they do not, in fact, appear until one or two of the leaves of the plumule are cut off, and the embryo is approaching maturity. The plerome of the root is continuous with that of the cotyledon and that of the stem; the cortex and dermatogen of the root are continuous with the periblem of the embryo. A cross-section of the embryo through the region of the root shows a rather large central plerome-complex, as yet undifferentiated, surrounded by a periblem two or three cells in thickness, the outermost layer of which is beginning to take on the characters of epidermis. Surrounding all of these are one or two rows of cells which are the sub-epidermal cells of the embryo, enclosed in the dermatogen of the embryo.

A somewhat older embryo shows the third stage of growth, that is, the elongation of that part of the embryo within which is the root. This exhibits at the same time a further differentiation of the tissues of the root. A greater number of cells than before has now been cut off from the initials which give rise to the root-cap (by which this organ is very well marked) and to the extra-plerome root tissues. The plerome initials also have become well defined.

The tissues of the radicle correspond to those of the root-tip of the mature plant, and agree closely with those of *Hordeum* figured by Strasburger (1898). The region below the root-cap is made of large, irregular cells, with little protoplasmic contents. These form the coleorhiza of the mature embryo.

After the epiblast has been cut off, there appears on the cotyledonary side of the plumule, and just within the ridge of tissues spoken of above as surrounding the stem-apex

(p. 348), an outgrowth which partly and later entirely encircles it. This is the plumule-sheath. Subsequently a leaf, the first one, appears on the side of the stem-apex opposite the cotyledon, which agrees with the position of the first leaf in *Hordeum* (Lermer and Holzner, 1888). The plumule and first leaf thus appear precisely as the leaves in the mature plant, alternating on the stem.

The homologies of the scutellum, epiblast, and plumule-sheath have been abundantly discussed by many writers (see Introduction), and will only be touched upon in this paper. The scutellum is generally regarded as the cotyledon. Some authors (1) believe the epiblast to be part of the cotyledon, (2) others that it is simply a projection of the nature of a trichome from the hypocotyl, and (3) still others as a second rudimentary cotyledon. The plumule-sheath has been explained in various ways: (1) it is looked upon as an outgrowth of the hypocotyledonary internode, (2) it is regarded as a third leaf alternating with the epiblast, and (3) finally as a ligule-like growth proceeding from the scutellum. My observations on the embryo of *Avena* lead me to agree with Kennedy (l. c.) in his interpretation of the homologies of the epiblast and of the plumule-sheath. That is, the epiblast can probably be considered to be a second cotyledon, although it is not homologous to the true cotyledon, and the plumule-sheath may be regarded to be a ligule-like growth proceeding from the base of the cotyledon, forming an integral part of it, and to be homologous to the ligule of the grass blade.

While the plumule and plumule-sheath are forming and about the time of the growth in the region of the radicle (referred to as the third period of growth), the cotyledon begins to increase in length and in breadth to form the scutellum of the mature embryo. An examination of the epidermis on the side of the cotyledon next to the endosperm shows that the palisade-like cells, which are characteristic of the dermatogen of the scutellum in grasses, are already formed. These cells in *Hordeum* (Lermer and Holzner, 1888) exude an enzyme which dissolves the starch and proteids of the endosperm and renders them

capable of being absorbed by the embryo in its germination. My attention has been called to the great similarity in appearance and in function between the epithelial cells of the scutellum of grasses and the cells at the tips of haustoria in certain phanerogamic parasites. The likeness between them and the epidermal cells in the haustorium of the Yellow Dodder is striking (Peirce, 1893). Both are epidermal cells modified to extract food from foreign tissues, and both exude solvents which can dissolve carbohydrates and proteids. A further and more careful comparison would be of importance, and might lead to some definite knowledge as to the reason of the peculiar parasitic habit assumed by the cotyledon of grasses.

As the region below the stem-apex increases in length, the epiblast, which was at first connected intimately with the plumule-sheath, becomes more and more removed from it toward the radicle end of the embryo. The epiblast increases somewhat in size although it is never as conspicuous an organ in *Avena* as in many other grass embryos. The epiblast is composed wholly of large parenchymatous cells and has no traces of conducting tissue.

VII. SUMMARY.

The principal points in this paper may be summarized as follows:—

- I. (a). The spikelet branches sympodially, the flower and finally the ovary terminating the parent axis.
- (b). The lodiculæ and the upper palet originate in the same rudiment.
- (c). The awn of the lower glume appears before its lamina, the latter being an outgrowth from it. Thus the origin of the parts of the lower glume resemble that of the blade and ligule of the vegetative leaf.
- (d). There is but a single carpel. This originates on the anterior side of the floral apex, which it encircles and finally encloses.

- (e). According to the hypothesis put forward in this paper, attempting to explain the meaning and homologies of the lodiculæ in the flower of *Avena*, they are to be considered as homologous to the stipular lodiculæ of the rye. Perianthal lodiculæ are not present in the flower of the oat.
- II. (a). The earlier growth of the stamen is mainly intercalary in the anther; immediately before the pollen is shed the filament elongates and causes the anther to protrude from the flower.
- (b). The archesporium is composed of a single row of cells originating in the periblem.
- (c). Each spore mother-cell reaches to the tapetum; none being bounded only by its fellows.
- (d). In the young anther three concentric rows of cells intervene between the loculus and the epidermis. Of these the tapetum and the middle series are resorbed, and the endothecium persists to form with the dermatogen the anther wall.
- (e). In the mature pollen-spore the generative nucleus has already divided.
- III. (a). The archesporium of the embryo-sac is of hypodermal origin.
- (b). The sister cells (potential macrospores) are variously formed. The nucleus of the archesporial cell divides to form four sister nuclei. These may be separated as soon as formed by cell-walls, or (2) they may somewhat later be separated by the subsequent formation of walls, or (3) they may never become separated, walls never forming.
- (c). The lowest sister cell becomes the macrospore.
- (d). There are no tapetal cells in *Avena*.
- (e). The antipodals multiply before fertilization of the egg to the number of 36 or more, and disappear as the endosperm develops.

- IV. (*a*). The synergidæ serve to nourish the young embryo.
- (*b*). The lumen of the embryo-sac begins to fill first in the region of the embryo.
- (*c*). All but one or two layers of cells of the nucellus are resorbed by the developing embryo-sac.
- (*d*). The outer integument of the ovule is destroyed; the inner persists as the seed-coat.
- V. (*a*). The first two cell-walls (which mark off the proembryo) in the development of the embryo appear in basipetal succession, and show the three "Types" of Nörner.
- (*b*). The cotyledon and the stem-apex are derived from the distal segment of the proembryo; the root, the root-cap and the periblem initials of the root from the middle segment; and the coleorrhiza from the basal segment.
- (*c*). The suspensor is separated from the embryo by the fourth wall; it does not subsequently divide.
- (*d*). The primary tissues are cut off in the first and second segments only; the divisions of the third segment are very irregular.
- (*e*). The organs of the embryo originate in the distichous manner characteristic of the vegetative leaves of grasses.
- (*f*). The scutellum appears to be analogous to the haustoria of certain phanerogamic parasites.

In conclusion I desire to express my gratitude to the officers of the botanical department, to Dr. D. H. Campbell in particular, for helpful advice and encouragement to me while pursuing the study of *Avena*. I ought to add also that the work was nearly but not quite finished prior to Dr. Campbell's departure for Europe in June.

STANFORD UNIVERSITY,
August 31, 1899.

BIBLIOGRAPHY.

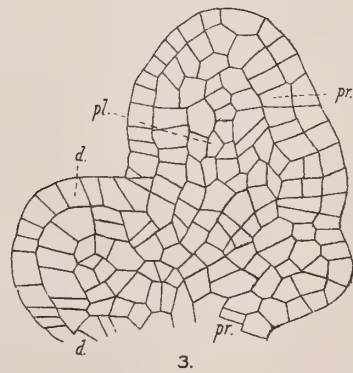
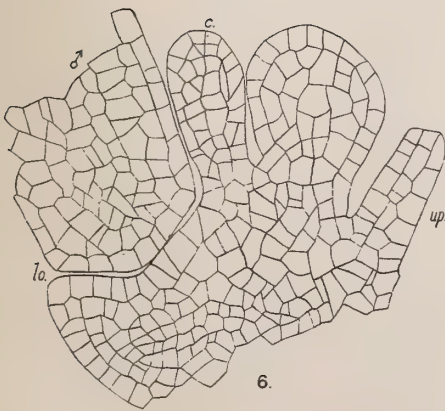
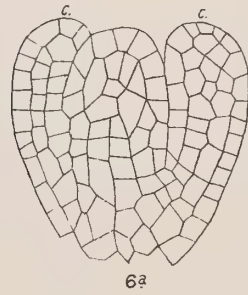
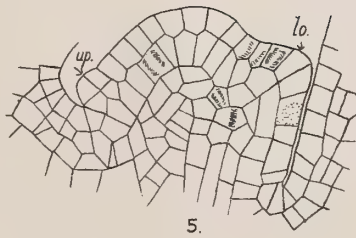
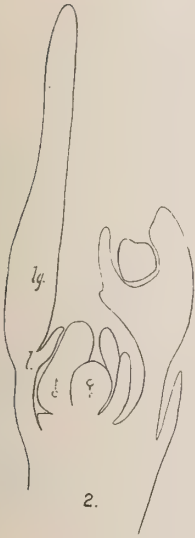
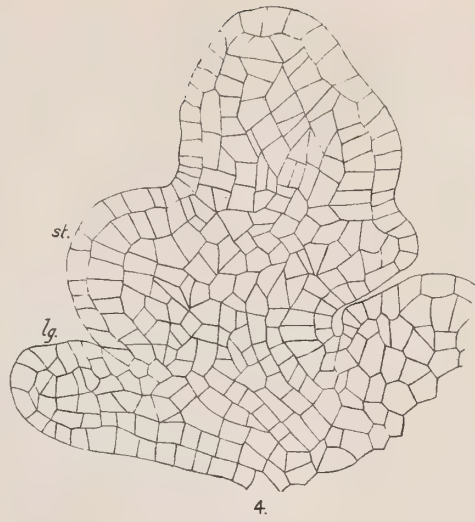
1892. BENTHAM, GEORGE. *British Flora*. 4th. Ed. 1.
 1892. BRUNS, DR. ERICH. Der Grasembryo. *Flora*, 1892.
 1897. CAMPBELL, D. H. A Morphological Study of Naias and Zannichellia. *Proc. Cal. Acad. Sci.*, 3d Ser., (Bot.) Vol. I, No. 1.
 1898. ———. Development of Lilæa. *Ann. of Bot.*, Vol. XII, pp. 1-28. March, 1898.
 1899. ———. Notes on the structure of the embryo-sac in Sparganium and Lysichiton. *Bot. Gaz.*, Vol. XXVII, March, 1899.
 1899a. ———. Studies on the Flower and Embryo of Sparganium. *Proc. Cal. Acad. Sci.*, 3d Ser., (Bot.) Vol. I, No. 9.
 1883. DE CANDOLLE, A. L'Origine des Plantes Cultivées. 1883.
 1820. CASSINI, H. L'Analyse de l'embryon de Gramineæ. *Journ. de Physique*, 1820. T. XCI.
 1897. CELAKOVSKY, L. J. Ueber die Homologien des Grasembryos. *Bot. Zeit.*, Bd. LV, pp. 141-174.
 1897. CHAMBERLAIN, CHARLES J. Contribution to the Life History of Lilium Philadelphicum. 2. The Pollen Grain. *Bot. Gaz.*, Vol. XXIII, August, 1897.
 1875. EICHLER, A. W. Blüthendiagramme. Leipzig, 1875.
 1880. FISCHER, A. Zur Kenntniss der Embryosacentwicklung einiger Angiospermen. *Jenaische Zeitschrift*, Bd. XIV, p. 90, 1880.
 1788. GÄRTNER, J. De fructibus et seminibus Plantarum, 1788.
 1881. HACKEL, E. Untersuchungen über die Lodiculæ der Gräser. *Engler's Bot. Jahr.*, Bd. 1. p. 336.
 1887. ———. Gramineæ. *Engler and Prantl's Nat. Pflanzenf.* Theil II, Abth. 2, 1887.
 1899. KENNEDY, P. BEVERIDGE. The Structure of the Caryopsis of Grasses with Reference to their Morphology and Classification. *Bull., U. S. Dept. of Agric.*, No. 19, 1899.
 1896. KOERNICKE, MAX. Untersuchungen über die Entstehung und Entwicklung der Sexualorgane von Triticum. *Verhandl. d. naturhistor. Vereins d. preuss. Rheinlande, etc.*, Jahr. LIII, p. 149, 1896.
 1888. LERMER UND HOLZNER. Beiträge zur Kenntniss der Gerste. Munich, 1888.
 1881. NÖRNER, CARL. Beiträge zur Embryoentwicklung der Gramineen. *Flora*, 1881. No. 16.
 1893. PEIRCE, GEORGE J. On the Structure of the Haustoria of Some Phanerogamic Parasites. *Ann. of Bot.*, Sept. 1893.
 1898. ROWLEE, W. W. The Morphological Significance of the Lodicules of Grasses. *Bot. Gaz.*, Vol. XXV, March, 1898.

1897. SCHAFFNER, J. H. Contribution to the Life History of *Sagittaria variabilis*. *Bot. Gaz.*, Vol. XXIII, April, 1897.
1897. ———. The Development of the Stamens of *Typha latifolia*. *Bot. Gaz.*, Vol. XXIV, August, 1897.
1898. SMITH, W. R. A Contribution to the Life History of the Pontederiaceæ. *Bot. Gaz.*, Vol. XXV, May, 1898.
1884. STRASBURGER, EDUARD. Neue Untersuchungen über den Befruchtungsvorgang bei den Phanerogamen. Jena, 1884.
1898. ———. Lehrbuch der Botanik. Third edition. Jena, 1898.
1895. VINES, S. H. Students' Text Book of Botany.
1880. WATSON, S. Botany of California, Vol. II. Geol. Sur. Calif., 1880.

EXPLANATION OF PLATE XLIX.

(Reduced about one-third).

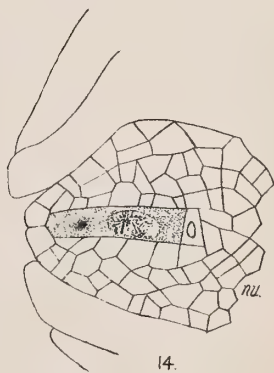
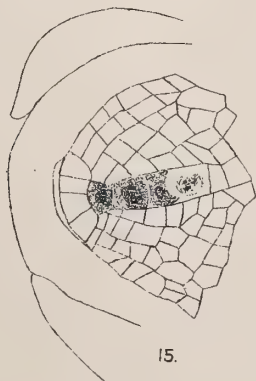
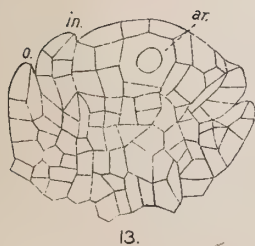
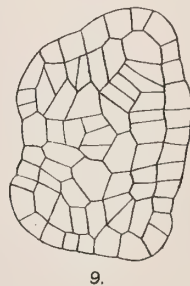
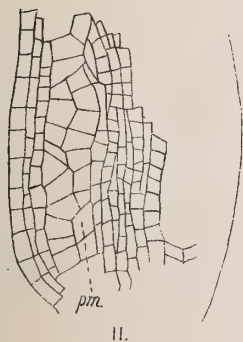
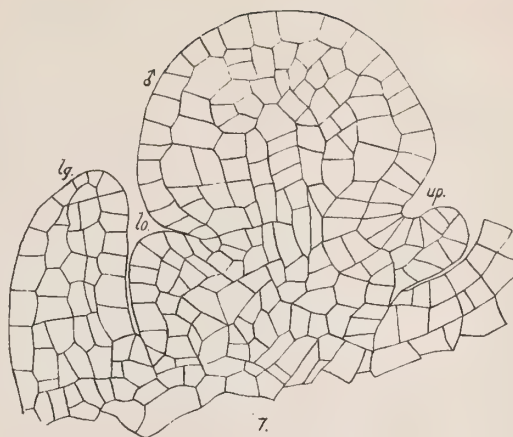
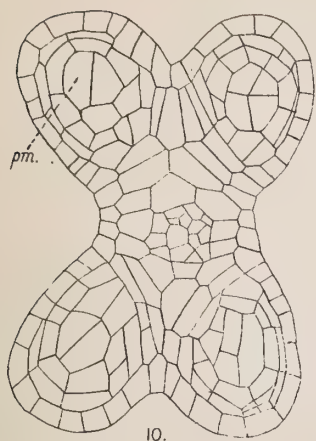
- Fig. 1. Longitudinal section of a young spikelet: $\times 57$; *lg*, lower glume; *c*, carpel; ♀, young ovary; ♂, young stamen.
- Fig. 2. Section of older spikelet to show the beginning of the lamina of the lower glume: $\times 57$; *l*, lamina; other lettering as in fig. 1.
- Fig. 3. Median longitudinal section of the primordium of a spikelet: $\times 320$; *d*, dermatogen; *pr*, periblem; *pl*, plerome.
- Fig. 4. A similar section, not quite median, showing an older floral rudiment: $\times 320$; *st*, floral apex; *lg*, lower glume.
- Fig. 5. Longitudinal section of apex of flower in which the upper palet (*up*) and lodiculæ (*lo*) appear: $\times 320$.
- Fig. 6. Longitudinal section of floral apex: $\times 320$; lettering as above.
- Fig. 6a. Longitudinal section of young ovule with carpel (*c*): $\times 320$.



EXPLANATION OF PLATE L.

(Reduced about one-fourth).

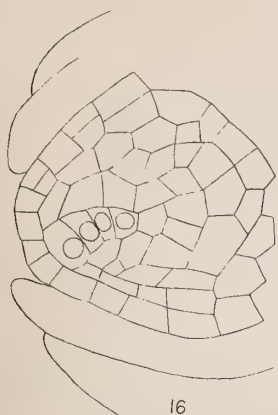
- Fig. 7. Longitudinal section, not median, of young flower showing a lodicula, and stamen: $\times 320$; lettered as above.
- Fig. 8. Cross-section of a young stamen: $\times 320$.
- Fig. 9. Cross-section of a somewhat older stamen than that represented in the preceding figure: $\times 320$.
- Fig. 10. Cross-section of stamen showing pollen mother-cells (*pm*): $\times 320$.
- Fig. 11. Longitudinal section of stamen of the age shown in the preceding figure: $\times 320$.
- Fig. 12. Section of pollen grain showing one vegetative and two generative nuclei: $\times 320$.
- Fig. 13. Longitudinal section of ovule: $\times 320$; *o*, outer integument; *in*, inner integument; *ar*, archesporial cell.
- Fig. 14. An ovule with nucellus (*nu*); and archesporial nucleus that has divided once (forming two sister nuclei): $\times 320$.
- Fig. 15. Four sister nuclei: $\times 320$.



EXPLANATION OF PLATE LI.

(Reduced about one-fourth).

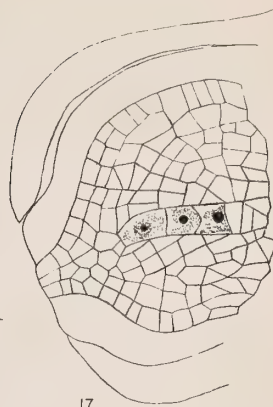
- Fig. 16. Four sister cells in which cell-wall formation accompanied nuclear division: $\times 320$.
- Fig. 17. Sister cells of which the outermost, which shows in the adjacent figure (17*a*), has been absorbed: $\times 320$.
- Fig. 18. Sister cells of which the outermost has been consumed: $\times 320$.
- Fig. 19. Longitudinal section of an ovule in which the macrospore has nearly absorbed the two middle sister cells: $\times 320$.
- Fig. 20. A four-celled embryo-sac: $\times 320$.
- Fig. 20*a*. Nucleus belonging to embryo-sac figured above.
- Fig. 21, 21*a*. An eight-celled embryo-sac in which the polar nuclei are approaching each other: $\times 320$; *ant*, antipodal cells; *e*, egg; *syn*, synergidæ; *p*, polar nuclei.



16



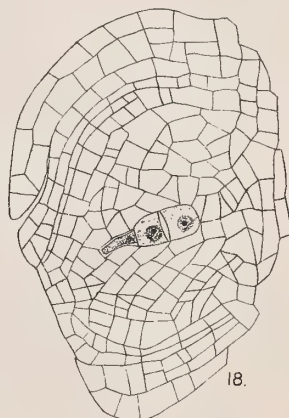
17a



17.



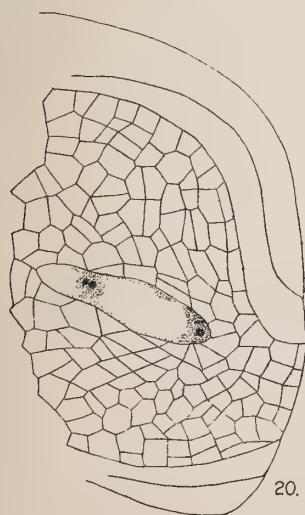
21.



18.



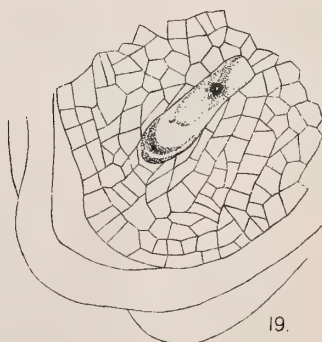
21a



20.



20a



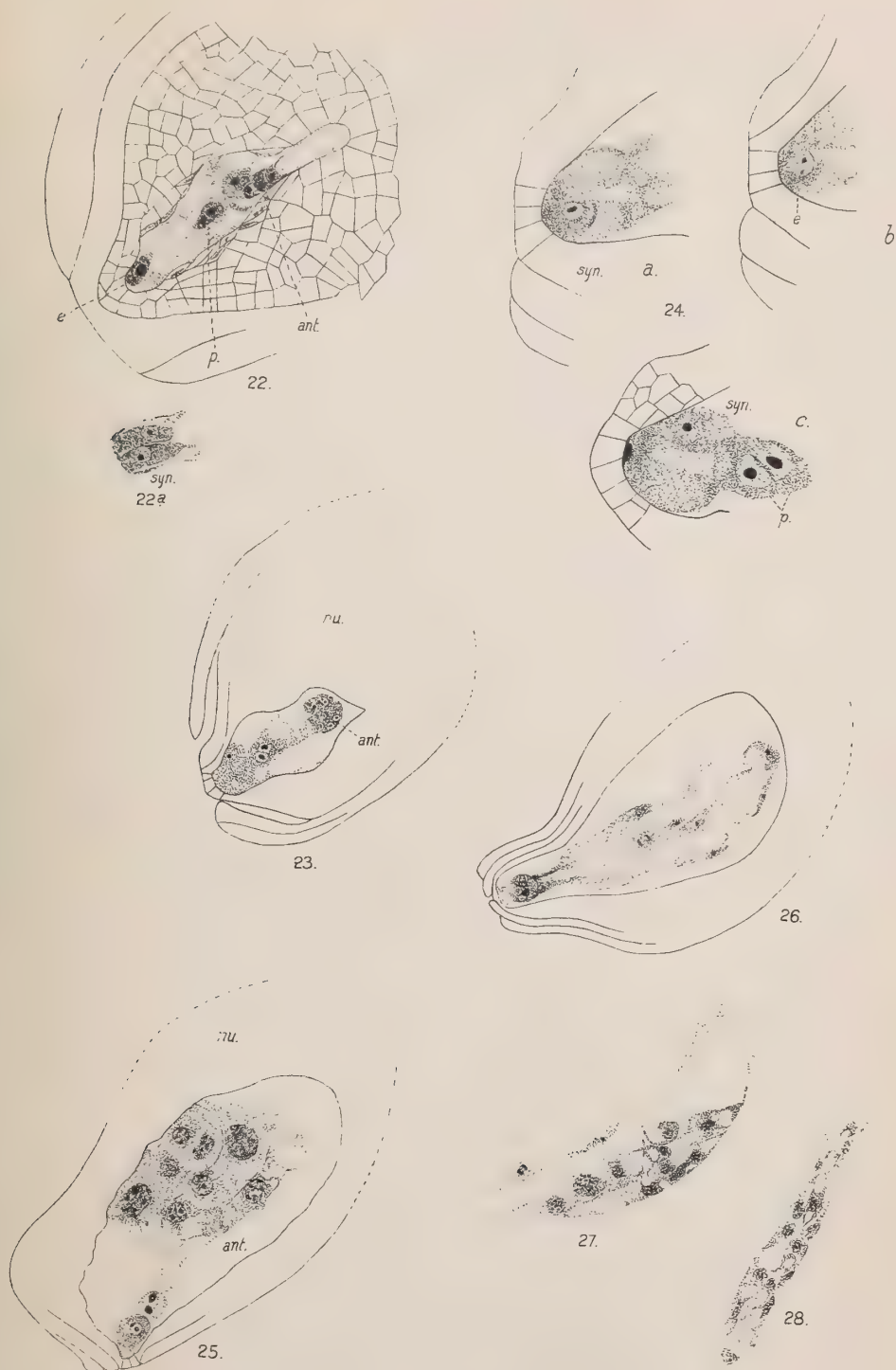
19.

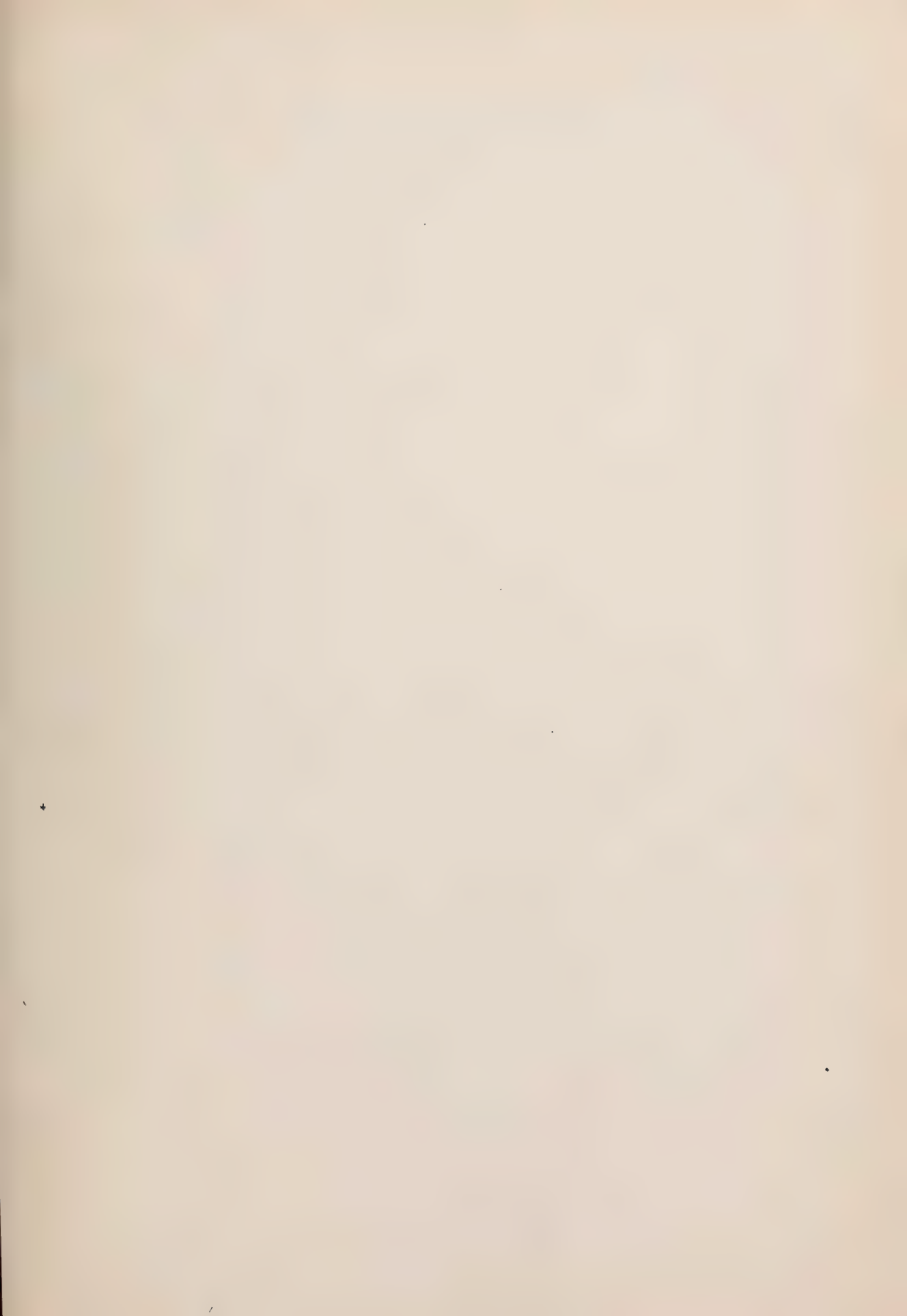


EXPLANATION OF PLATE LII.

(Reduced about one-fourth).

- Fig. 22. Embryo-sac showing the beginning of the multiplication of the antipodals: $\times 320$; synergidæ in the adjoining figure.
- Fig. 22a. Synergidæ of fig. 22.
- Fig. 23. An embryo-sac with young antipodal complex; shows the relation of the embryo-sac to the nucellus: $\times 110$.
- Fig. 24. Detail of egg-apparatus: $\times 320$; polar nuclei not yet fused.
- Fig. 25. A longitudinal section of ovule showing nucellus, embryo-sac, one-celled embryo, and the first division of the endosperm nucleus: $\times 110$.
- Fig. 26. An ovule with nucellus, two-celled embryo, and dividing endosperm nuclei: $\times 57$.
- Fig. 27. Antipodal complex of the embryo-sac shown in the preceding figure: $\times 80$.
- Fig. 28. Antipodals that are undergoing disintegration: $\times 80$.

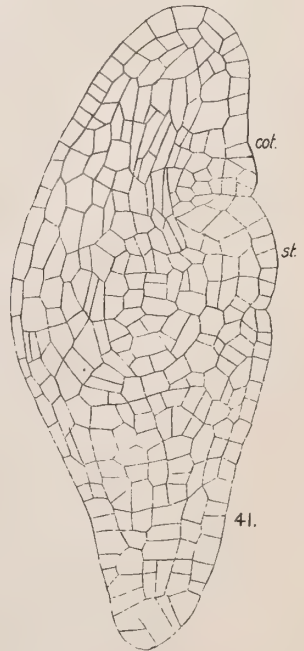
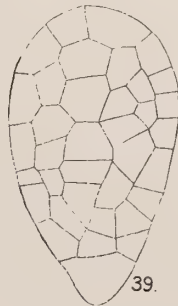
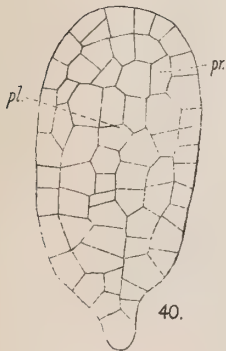
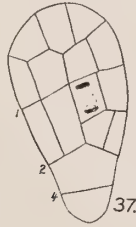
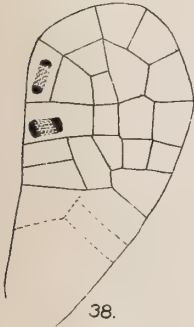
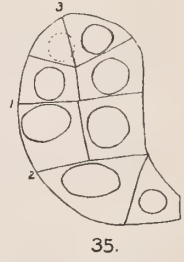
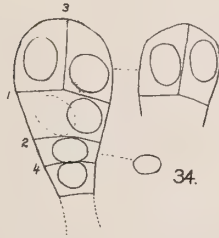
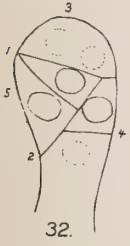
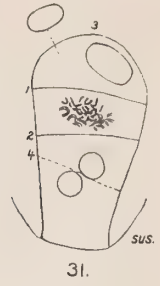
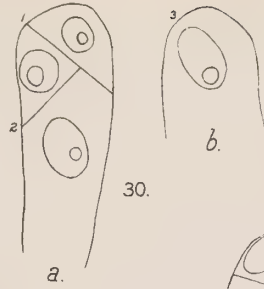




EXPLANATION OF PLATE LIII.

(Reduced about one-third).

- Fig. 29. First division of the embryo: $\times 430$.
Fig. 30a, b. Four-celled embryo; "Type III" of Nörner: $\times 430$.
Fig. 31. Basal cell of embryo has divided to form the suspensor; "Type I" of Nörner: $\times 430$.
Fig. 32. Same stage as fig. 31; "Type II" of Nörner: $\times 430$.
Fig. 33. Seven-celled embryo; dotted lines indicate the connection of the embryo to the micropyle: $\times 430$.
Fig. 34. Embryo in which quadrants have formed in the first segment: $\times 430$.
Fig. 35. Embryo in which octants have formed in the first segment, quadrants in segment two, while the third segment has divided but once: $\times 430$.
Fig. 36. Separation of plerome in the second segment: $\times 430$.
Fig. 37. Differentiation of the plerome in the first two segments: $\times 320$.
Fig. 38. Cutting off of the dermatogen: $\times 430$.
Fig. 39. Section nearly median of young embryo, in which the primary tissues are cut off: $\times 400$.
Fig. 40. Somewhat older embryo than that shown in the preceding figure: $\times 320$.
Fig. 41. Nearly mature embryo; *st*, stem; *cot*, cotyledon; *r*, root: $\times 280$.
Fig. 42. Cross-section of older embryo with the wings of the scutellum, the plumule sheath, and young leaves showing: $\times 140$.



PROCEEDINGS OF THE ACADEMY.

(OCTAVO.)

Third Series.

BOTANY.

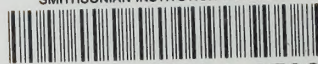
VOL. I.

No. 1—A Morphological Study of Naias and Zannichellia. By Douglas Houghton Campbell	\$1.00
No. 2—Studies in the Herbarium and the Field.—No. 1. By Alice Eastwood	.25
No. 3—Studies in the Herbarium and the Field.—No. 2. By Alice Eastwood	.50
No. 4—Phycological Memoirs. By De Alton Saunders	.75
No. 5—Some Observations on the Development of the Karyokinetic Spindle in the Pollen-Mother-Cells of Cobæa scandens Cav. By Anstruther A. Lawson	.35
No. 6—The Origin of the Karyokinetic Spindle in Passiflora coerulea Linn. By Clara L. Williams.	.35
No. 7—The Nature of the Association of Alga and Fungus in Lichens. By George James Peirce	.35
No. 8—Californian Hypogæous Fungi. By H. W. Harkness	.75
No. 9—Studies on the Flower and Embryo of Sparganium. By Douglas Houghton Campbell	.50
No. 10—A Morphological Study of the Flower and Embryo of the Wild Oat, Avena fatua L. By William Austin Cannon	.50

All subscriptions, applications for exchanges, and inquiries concerning the publications should be addressed to

J. O'B. GUNN, Corresponding Secretary,
California Academy of Sciences,
San Francisco, California.

SMITHSONIAN INSTITUTION LIBRARIES



3 9088 00614 9793